# New Occurrences of Culmacanthid Acanthodians (Pisces, Devonian) from Antarctica and southeastern Australia

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Two new species of the acanthodian lish Culmacanthus Long 1983 are described from the lower part of the Aztec Siltstone of southern Victoria Land. Antarctica, and Facies 3 of the Boyd Volcanic Complex of southeastern New South Wales. Both are represented only by check plates. That of *C. antarctica* sp. nov. has distinctive ornament, a longer lateral than dorsal lamina, and the infraorbital sensory groove passing off the ventral margin of the plate. *C. pambulensis* sp. nov. resembles the type species *C. stewarti* Long in the shape of the posterior margin of the check plate and the ventral course of the infraorbital sensory canal, but differs in its proportions, the shape of the anterior margin, and the much finer dermal ornament. *C. antarctica* sp. nov. is considered to be the oldest (?late Middle Devonian) because it is associated with turiniid thelodont scales. The two other species of *Culmacanthus* occur with bothriolepid and phyllolepid placoderms in assemblages considered to be early Late Devonian (Frasnian). The specific differences described herein suggest however that they are not precise correlatives. Culmacanthid acanthodians are only known from southeastern Australia and southern Victoria Land, a distribution pattern previously noted in chondrichthyans and placoderms from the same faunas, and suggesting that *Culmacanthus* was an east Gondwanan endemic.

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## INTRODUCTION

The acanthodians are a major group of Palaeozoic gnathostome fishes, with a fossil record from Silurian to Permian. During the Devonian Period they were widely distributed in both non-marine and marine aquatic environments, and their tiny scales and characteristic fin-spines are commonly represented in microvertebrate assemblages. However articulated specimens are much less common, and knowledge of acanthodian morphology is based mainly on a few localities in Europe and North America which have yielded well-preserved complete specimens (for a comprehensive review of the group see Denison, 1979).

A. S. Woodward was the first to describe Australian acanthodians, from the Lower Carboniferous Mansfield group of Victoria (Woodward, 1906), and he also published the first descriptions of the group from Antarctica (Woodward, 1921). Isolated acanthodian scales and spines occur widely in Devonian rocks of eastern and central Australia (Fig. 1), and in recent years some well-preserved articulated acanthodians have been described from southeastern Australia (e.g. Long, 1983a, 1986a). The best-known locality is Mount Howitt in east central Victoria, which is the type locality for the genus *Culmacanthus* Long 1983, of which additional material is described in this paper. With these two new species the genus *Culmacanthus* is now known from three localities in southeastern Australia, and one locality in Antarctica (Fig. 1). Its distribution pattern matches that seen in several other taxa of Devonian fishes, the palaeogeographic significance of which is discussed below. All described specimens are housed in the Commonwealth Palaeontological Collection (prefix CPC), Bureau of Mineral Resources,



Fig. 1. Reconstruction of East Antarctica against Australia, modified from the Gondwana reconstruction of Lawver and Scotese (1987). showing the main localities of Devonian acanthodian fishes in the southwest Pacific region. Numbered localities are the only known occurrences of culmacanthid acanthodians, as dealt with in this paper; 1, Mount Crean, Lashly Range, southern Victoria Land (*Culmacanthus antarctica* sp. nov.); 2, Mount Howitt, east central Victoria (*Culmacanthus stewarti* Long); 3, Freestone Creek, east Gippsland, (culmacanthid indet.); 4, Pambula River, southeastern New South Wales (*Culmacanthus pambulensis* sp. nov.). Other abbreviations are: B, Broken River, Queensland; BD, Burrinjuck Dam, New South Wales; C, Cobar area, Darling Basin; DS, Duleie Syncline, Georgina Basin, EM, Crashsite Quartzite, Ellsworth Mountains; G, Grampians, western Victoria; H, Horlick Formation, Ohio Range; M, Munyarai, Officer Basin; MBL, Marie Byrd Land, West Antarctica; MR, Maedonnell Range, Amadeus Basin; NNZ, New Zealand, North Island; R, Recfton, New Zealand, South Island; RS, Ross River Syncline, Amadeus Basin; T, Tasmania; TS, Toko Syncline, Georgina Basin; WC, Wilson Cliffs, Canning Basin.

Geology and Geophysics, Canberra, A.C.T. Material of the type species *Culmacanthus* stewarti Long is housed in the Museum of Victoria (prefix NMP).

## PREVIOUS INVESTIGATIONS

The first samples of the Antarctic Aztec fish fauna were collected by F. Debenham on the British Antarctic 'Terra Nova' expedition of 1910-13, from moraine material at Granite Harbour on the coast of southern Victoria Land. They were described by Woodward (1921), who identified eight taxa of Devonian fishes, including isolated acanthodian scales which were said to resemble those of *Cheiracanthus murchisoni* from the Middle Devonian of Scotland. In situ remains of the Aztec fauna were not discovered until the Trans-Antarctic Expedition of 1955-58 (see Gunn and Warren, 1962), when Devonian fish remains were collected from the Aztec Siltstone at three localities (Lashly Mountains, Mount Feather, Boomerang Range) in the region of the Skelton Névé of southern Victoria Land (locality 1, Fig. 1). Other fish remains from the same general area were recorded by Matz and Hayes (1966) and Matz, Pinet and Hayes (1972; their 'Fortress Formation') from west Beacon Heights, Mount Fleming, Mount Crean, and Aztec Mountain, and by Helby and McElroy (1969) from Aztec Mountain. Gunn and Warren's collection was described by White (1968). The most extensive collections of Devonian fishes from the Aztec Siltstone were made by Antarctic expeditions from Victoria University of Wellington in 1968-69 (see McKelvev et al., 1972), and in 1970-71 (VUWAE 15), when the specimen described below was collected. Detailed measured sections through the Aztec Siltstone at most of the fossil localities are given in Askin et al. (1971) and Barrett and Webb (1973). Recent publications dealing with or discussing the Aztec fish fauna include Ritchie (1971a, b, 1974, 1975). Young (1982, 1988), and Grande and Eastman (1986). A detailed locality map and a summary of the 24 known localities for the Aztec Siltstone fish fauna are given in Young (1988).

In the material collected by Gunn and Warren, White (1968) identified several types of acanthodian spines. Ribbed spines from the upper fossiliferous horizon in the Boomerang Range were referred to a new species (*G. warreni*) of the genus *Gyracanthides*, originally described by Woodward (1906) from the Early Carboniferous of Mansfield in Victoria. A new genus and species (*Antarctonchus glacialis* White) was erected for long slender acanthodian spines with numerous strong longitudinal ribs. White also determined as an acanthodian some small spine fragments originally described by Woodward (1921) as an antiarch (*Byssacanthoides debenhami* Woodward). In addition to these named taxa from the Middle-Late Devonian, V. T. Young (1986) has referred to the genus *Machaeracanthus* two types of Early Devonian acanthodian spines from the Horlick Formation in the Ohio Range of the southern Transantarctic Mountains, and a similar specimen is recorded from the Ellsworth Mountains (H, EM, Fig. 1).

In southeastern Australia acanthodian remains have been known from Victoria for some time (Woodward, 1906; Hills, 1931). More recently Long (1983a) described *Culmacanthus stewarti* from the Mount Howitt fish locality, and figured one incomplete specimen from Freestone Creek in eastern Victoria as a probable culmacanthid (localities 2, 3, Fig. 1). A second acanthodian from the Mount Howitt fauna (*Howittacanthus*) was described by Long (1986a). A summary of the Victorian Devonian fish localities and their biostratigraphy is given in Long (1983b: fig. 1). Placoderms associated with *Culmacanthus* are also described by Long (1984) and Long and Werdelin (1986).

Over the state border, in southeastern New South Wales, Devonian fish remains were discovered in the Eden-Pambula area in 1978 (locality 4, Fig. 1), and a preliminary report (Young, in Fergusson *et al.*, 1979) identified four assemblages ranging in age probably from latest Middle Devonian (Givetian) through to the end of the Late Devonian (Famennian). One specimen, first described as a possible osteichthyan plate (Fergusson *et al.*, 1979: 103), is referred below to *Culmacanthus* on the basis of Long's (1983a) description of this genus. Further collecting in 1979 produced the new specimens described below. Other described elements of the Devonian fish faunas from the south coast of New South Wales include sharks from the Bunga Beds near Bermagui (Young, 1982), and an asterolepid antiarch from the Pambula River area (Young, 1983). Elements still to be described include bothriolepid and remigolepid antiarchs, phyllo-

lepid placoderms, and rhipidistian and other acanthodian remains. A locality map of the region is given in Young (1983: fig. 1).

## SYSTEMATIC DESCRIPTIONS Subclass ACANTHODII Owen Order CLIMATIIDA Berg Suborder DIPLACANTHOIDEI Miles 1966 Family CULMACANTHIDAE Long 1983 Genus *Culmacanthus* Long

Remarks: The above taxa are defined in Denison (1979) and Long (1983a).

Culmacanthus antarctica sp. nov. (Figs. 2A, 3A)

1986a. 'culmacanthid cheek plates' (pars) Long, p. 13.

Holotype: CPC 26579, a right cheek plate preserved in part and counterpart.

Locality: Mount Crean, east side of the Lashly Range (77° 53'S, 159° 33'E), southern Victoria Land, Antarctica (locality 8 of Young, 1988: fig. 3).

Horizon: From the lower part of the Aztec Siltstone, within 40 m of the base of the formation (unit 5 of section L2 measured by Askin *et al.*, 1971; for a detailed discussion of the stratigraphy of the Mount Crean section see Young, 1988).

**Diagnosis:** A *Culmacanthus* possessing a cheek plate in which the infraorbital sensory canal passes off the ventral margin, the anteroventral corner is pronounced, the ventral lamina is longer and deeper than the dorsal lamina, and the plate is fairly flat, ornamented with closely spaced ridges and elongate tubercles with a flat external surface, and has a breadth/length index of about 79.

**Remarks:** Long (1983a) did not present a diagnosis for the type species *C. stewarti*, but compared to the Antarctic specimen there are obvious differences in the form of the cheek plate. In the type species the coarser ornament of more widely spaced ridges have a rounded rather than flat dorsal surface, the anterior margin of the plate is distinctly notched (Fig. 3B), there is a more pronounced angle between the dorsal and lateral laminae, the dorsal lamina is longer than the lateral, and the latter has a concave external surface. The most obvious difference is in the course of the main sensory groove, with both dorsal and ventral sections passing off the anterior margin of the plate.

The articulated remains of *C. stewarti* show that *Culmacanthus* was a diplacanthoid acanthodian with two dorsal fin-spines, paired pectoral and pelvic spines, and an anal spine (Fig. 5). These spines are ornamented with approximately nine coarse longitudinal ribs, and they have a deeply inserted base which is finely striated (Long, 1983a). It is possible therefore that some of the similar acanthodian spines from the Aztec Siltstone named by White (1968) as *Antarctonchus* may also belong to *Culmacanthus*. Long (1983a) has already suggested this for the isolated spines from Freestone Creek in Victoria named *Striacanthus* by Hills (1931). However, in the absence of articulated material demonstrating this, and because the histology of *Culmacanthus* spines is at present unknown, I follow Long's (1983a) procedure here, and leave *Antarctonchus* as a form genus for isolated spines, until such time as new material or more detailed study can demonstrate that the spines and dermal cheek plates come from the same fish.

**Description:** The holotype and only referred specimen is an isolated dermal check plate preserved in part and counterpart. The external impression was cleaned in dilute hydrochloric acid to remove the bone, and the distinctive ornament is well displayed in a latex cast (Fig. 2A). The counterpart is preserved as bone except for the posterolateral corner, which is an impression of the visceral surface. All margins of the plate are

PROC. LINN. SOC. N.S.W., 111 (1), 1989



*Fig. 2.* Right check plates of *Culmacanthus* in external view (latex casts whitened with ammonium chloride). **A**, *C. antarctica* sp. nov., holotype, CPC 26579 (x4). **B-D**, *C. pambulensis* sp. nov.; **B**, holotype, CPC 26580 (x4); **C**, CPC 26581 (x3); **D**, CPC 26582 (x4).

complete. The orientation of such isolated cheek plates is not readily determined, but following the work of Long (1983a) on the articulated Mount Howitt material of *C. stewarti*, the position of the short sensory groove (ifc.b, Fig. 3A) shows this to be a right dermal cheek plate. It is about 21.5mm long, and relatively deep (breadth/length index of 79). The anterior margin lacks the distinct orbital notches seen in the type species (Fig. 3B), and slopes anteroventrally to a pronounced anteroventral corner, behind which the infraorbital sensory groove passes off the ventral margin of the plate.

The plate has a slight flexure at the level of the posterior angle of the infraorbital sensory groove (ifc, Fig. 3), as previously described by Long (1983a), but overall it is a much flatter plate than in the Victorian species (based on NMP 159838). The inflexion of the infraorbital groove is placed high on the plate, which gives it a much larger lateral than dorsal lamina. The short posterodorsal sensory groove (ifc.b), as described for *C. stewarti*, was interpreted by Long (1983a) as possibly part of the preopercular sensory groove, but this groove in fishes normally passes posterolaterally across the cheek towards the mandibular joint. It is considered more likely that the short groove on the

cheek plate of *Culmacanthus* is equivalent to the 'postero-median branch of the infraorbital canal' of *Diplacanthus* identified by Watson (1937; 'central sensory line' of Miles, 1966).



Fig. 3. Cheek plates of Culmacanthus restored in external view. A, a right plate of C. antarctica sp. nov., after the holotype, CPC 26579; B, C. stewarti Long, a left plate, restored after a latex cast of NMV P159838 (see Long 1983a: fig. 4B); C, a right plate of C. pambulensis sp. nov., after the holotype, CPC 26580. an, anterior notch; dep.p, posterior depression; ife, infraorbital sensory groove; ife.b, posterodorsal ('eentral') branch of infraorbital sensory groove; pn, posterior notch.

The distinctive ornament of C. antarctica sp. nov. comprises cusp-like tubercles which change into elongate ridges towards the posterior margin. In front of the sensory groove the surface of each cusp slopes upwards from the bone surface in a posterodorsal direction, at which a point may be developed, to give some cusps a triangular shape. Behind the sensory groove the more elongate cusps and short ridges have their pointed ends directed posteriorly, and are separated by deep, narrow grooves. Most of the ridges and tubercles are ornamented with up to four very fine ridges which may branch towards the anterior. Typically the elongate primary ridges of the ornament which are most pronounced on the posterior half of the plate have a flat or slightly concave upper surface, with the edges clearly marked by two fine ridges. Compared to *C. stewarti* (NMP 159838, Fig. 3B) the ornament is more finely sculptured, with the ridges and tubercles more closely spaced. In the type species (Long, 1983a, fig. 4A, B) the ornament is

PROC. LINN. SOC. N.S.W., 111 (1), 1989

coarser, with wider intervening spaces, and scattered tubercles along the ventral margin. However some fine striations are also visible on the more elongate tubercles and ridges, and in larger specimens there are fewer tubercles and longer ridges (Long, 1983a, fig. 2**B**).

Culmacanthus pambulensis sp. nov. (Figs. 2**B-D**, 3**C**, 4)

1979. 'osteichthyan, with an ornament of delicate subparallel ridges' Young, in Fergusson et al., p. 103.

1983a. 'dermal cheek plate . . . from Pambula River' Long, p. 54. 1986a. 'culmacanthid cheek plates' (*pars*) Long, p. 13.



Fig. 4. Culmacanthus pambulensis sp. nov., check plates in external view. A, a right plate, after CPC 26581; B, a left plate, after CPC 26583. For abbreviations see caption to Fig. 3.

17

Name: Abbreviated from the nearby town of Pambula, N.S.W.

Holotype: CPC 26580, a right cheek plate.

Other Material: Right (CPC 26581, 26582) and left (CPC 26583) cheek plates, and another ornamented fragment (CPC 17004).

Locality: Grid Reference 7510È 59081N on the Pambula 1:25000 Sheet, about 5km west of the town of Pambula on the south coast of New South Wales (see Young, 1983: fig. 1).

**Horizon:** Facies 3 of the Boyd Volcanic Complex, as described by Fergusson *et al.* (1979). **Diagnosis:** A *Culmacanthus* possessing a fairly flat cheek plate in which the infraorbital sensory canal passes off the anterior margin, the anterior margin has only shallow or indistinct notches, the ventral lamina is considerably deeper than the dorsal lamina, the closely spaced ornament comprises fine ridges and elongate tubercles, and the breadth/length index varies between at least 68 and 94.

**Remarks:** Apart from the obvious and consistent differences in ornament, the three measurable specimens of *C. pambulensis* are broader than in the type species, although for the smallest example described below (CPC 26580) this difference is only slight. Long (1983a: 56) regarded such differences in proportion to be generic rather than specific features, but the variability in proportions is clear in this new species, and the other obvious similarities indicate that these specimens are properly referred to the genus. *C. pambulensis* resembles *C. antarctica* rather than *C. stewarti* in the flatter cheek plate, the longer and steeper disposition of the ventral section of the infraorbital sensory groove, and the absence or slight development of notches on the anterior margin. It differs from *C. antarctica* but resembles *C. stewarti* in the fact that the infraorbital groove passes off the anterior margin of the plate. Long (1983a) noted other specimens from Freestone Creek in eastern Victoria with broader proportions than the type species, as in *C. pambulensis* sp. nov., but that material is at present too poorly known to permit useful comparisons.

**Description:** All specimens are preserved as external moulds, which have been studied by latex casting. The holotype (Figs 2B, 3C) is the smallest specimen (length 14mm), and the most complete. The infraorbital groove has an attenuated ventral section, not seen in other examples, and interpreted as an individual variation. The posterodorsal branch is a short separate groove (ifc.b, Fig. 3C) as in other examples with this part preserved. Compared to C. stewarti (represented by NMP 159838) the cheek plate is rather flat. The lateral lamina is slightly concave near the posterior corner (dep.p), and there may be another shallow depression running anteroventrally beneath the ventral section of the infraorbital canal, but otherwise both laminae of the plate are gently convex. The posterior depression is seen in all available specimens of this species (Fig. 2B-D). Two larger specimens are unusually broad (Fig. 4), although their posterior margins are somewhat irregular. This may be due to incomplete preservation, but an irregular margin abutting against small plates at the posterior margin of the gill cover is considered more likely. It is possible that breadth of the plate increased allometrically with size, but evidence against this is provided by C. stewarti, where the largest plate (Long, 1983a: fig. 2) is also the most elongate (erroneously stated as 'twice as broad as long' by Long, 1983a: 56). In both CPC 26581 and 26583 the lateral lamina projects posteriorly, as in C. antarctica described above, and all specimens with the region preserved show a shallow notch on the posterodorsal margin (pn, Figs 3C, 4). The general similarity of the delicate ornament in the two largest examples (Figs 2C, 4B) to other specimens from this locality suggests that they are conspecific, and that proportions of the cheek plate are more variable than previously thought. In the type species only three cheek plates have been described, with two from one individual, so further material is required to assess the variability of this feature.

#### G. C. YOUNG

The ornament in *C. pambulensis* is much finer than in *C. antarctica* or *C. stewarti*. Small triangular tubercles with posterodorsally directed points predominate in front of the sensory canal, as in the other species, and behind the canal these tubercles become more elongate and posteriorly directed (Fig. 2B, D), and may coalesce into subparallel ridges (Figs 2C, 4B). Specimen CPC 17004 previously mentioned by Young (in Fergusson *et al.*, 1979) is referred to *C. pambulensis* only on its similar ornament, since no sensory grooves are preserved.

#### DISCUSSION

## Morphology and Systematics

Denison (1979) included two genera in his family Diplacanthidae - Diplacanthus Agassiz and Gladiobranchus Bernacsek and Dineley. Long (1983a) preferred to place Gladiobranchus as closely related to Uraniacanthus, as originally suggested by Bernacsek and Dineley (1977). However Bernacsek and Dineley supported this relationship by suggesting that Uraniacanthus may have possessed dermal plates and prepectoral spines, even though Miles (1973) expressed no doubt from detailed study of the specimens that these structures were absent in Uraniacanthus. Bernacsek and Dineley (1977) also inferred that Gladiobranchus had dentigerous jawbones, but the holotype shows anterior circumorbital bones, indicating proximity of the snout, but no sign of ossified jaw elements. These may have been lost, but the available evidence favours the interpretation that Gladiobranchus did not possess them. Supporting this, and the climatiid affinities of Gladiobranchus, are the presence of dermal shoulder plates, prepectoral spines, and the large plates and tesserae of the head (Denison, 1979). The scapulocoracoid of Gladiobranchus was restored by Bernacsek and Dineley (1977) as a low and broad element with a truncated dorsal end, but the specimen (Bernacsek and Dineley, 1977: pl. 7) suggests a higher narrow dorsal termination, with an anterior ridge and expanded posterior ventral part, just as in Diplacanthus. The two enlarged circumorbitals, one at the posterodorsal corner of the orbit, are special features shared with Diplacanthus, as Denison (1979) noted. Thus I follow Denison (1979) in considering Gladiobranchus better placed as a diplacanthoid acanthodian, rather than an ischnacanthid (see also Long, 1986b: 335).

Long (1983a) modified Miles's (1966) diagnosis of the Diplacanthoidei to include Culmacanthus. The most significant resemblances (Fig. 5) are in the large dermal cheek plate crossed by the infraorbital sensory groove, the relatively deep body, and the deeply inserted spines. Culmacanthus differs from Diplacanthus primarily in the larger size of the cheek plate, the absence of intermediate fin-spines, the probable absence of a mandibular bone, the high narrow scapulocoracoid, and the structure of the dermal shoulder girdle, with an unpaired lorical plate, and no spines attached to the paired pinnals. Long (1983a) suggested that the cheek plate of Culmacanthus may have been homologous to the postorbital or preopercular bones of Diplacanthus, but since there is no sensory groove passing posterolaterally across the plate it seems more likely that it is only a much enlarged postorbital, which extended more dorsally than the corresponding bone of Diplacanthus, to include the junction of the posterodorsal branch of the infraorbital canal at its ossification centre. For functional reasons it is likely that the cheek plate only covered the region of the palatoquadrate, with a flexible hyoid gill cover situated between it and the scapulocoracoid. The well-ossified branchiostegal rays in this position in Gladiobranchus may be interpreted as a symplesiomorphy, by outgroup comparison with climatiids. It is unclear from Long's (1986b) analysis of the dermal shoulder girdle of climatiids whether the condition in Culmacanthus is primitive or specialized, but if intermediate fin-spines and pectoral spines firmly attached to the pinnal plates are



Fig. 5. Culmacanthus stewarti Long. Restoration of complete fish, slightly modified after Long (1983a: fig. 9).

synapomorphies of 'higher climatiids' as he suggests (1986b: 337), then *Diplacanthus* would be more closely related to some Early Devonian climatiids than to *Culmacanthus*. All students of acanthodian evolution have acknowledged the small number of reliable characters available to define the major groups, and in the case of *Culmacanthus* the main evidence still to be forthcoming concerns the histology of the scales and fin spines. This is not known in the Victorian material because the bone is badly weathered. Better-preserved material permitting histological study can be expected to clarify the relation-ships of this form to the Euramerican diplacanthids.

## **Biostratigraphy**

A biostratigraphic analysis of the Aztec fish fauna based on the distribution of antiarchs was presented by Young (1988), in an attempt to resolve previous differences of opinion about its precise age. Woodward (1921) first proposed a Late Devonian age on the evidence of the antiarch Bothriolepis, and associated shark and large osteolepid scales, and Gross (1950) reached the same conclusion. However White (1968) noted the apparent mixing in the Aztec fauna of groups that elsewhere range in age from Middle or even Early Devonian, to Late Devonian or Early Carboniferous, and on this basis he favoured a late Middle Devonian rather than early Late Devonian age. Ritchie (1975) added the placoderms Phyllolepis and Groenlandaspis to the faunal list, and proposed a younger Late Devonian age. Young (1982) suggested correlations with southeastern Australia based on the sharks in the Aztec fauna, which were consistent with Helby and McElroy's (1969) assessment of a Frasnian age for a palynoflora dominated by the spore Geminospora lemurata. This species was assessed by Playford (1983) to have a known biostratigraphic range from early or middle Givetian to late Frasnian or early Famennian. However in Europe McGregor (1979) has estimated a much greater (Emsian-Famennian) range for the possibly synonymous Geminospora svalbardiae, so the spore evidence at present only dates the Aztec Siltstone within broad limits.

Other evidence supporting comparisons between the Aztec succession and the Devonian sequences of southeastern Australia include the acanthodian *Gyracanthides* described from Victoria by Woodward (1906), and from the upper Aztec succession by White (1968), the antiarch *Pambulaspis* from southeastern New South Wales (Young,

1983) and described by Young (1988) from the top of the Aztec, and the culmacanthid acanthodians just described. Culmacanthus antarctica is associated with turiniid thelodont scales and bothriolepid antiarchs, and may therefore be the oldest known species, since no thelodonts have been recorded from the successions in eastern Victoria and the south coast of New South Wales. Young (1988) noted that the association of bothriolepid antiarchs with thelodont scales is currently known from only one other locality, in the Hatchery Creek fauna from near Wee Jasper, New South Wales (Young and Gorter, 1981). A post-Emsian age for this fauna is indicated by conodonts in the underlying Murrumbidgee Group (serotinus Zone or slightly younger), but a younger age limit is uncertain. In contrast the two Australian species of Culmacanthus are associated with phyllolepid placoderms, which occur widely in southeastern Australia, in all other post-Emsian faunas currently known which contain placoderms. From eastern Victoria and the southern coast of New South Wales only the Bunga Beds fauna (Young, 1982) lacks phyllolepids, but this is an impoverished fauna in which placoderms have not been found. The abundant placoderms in the Aztec Siltstone includes phyllolepids only in the highest horizons, and Young (1988) suggested that the base of the phyllolepid zone preserved in the Aztec Siltstone, and the first appearance of the antiarch Pambulaspis, may be older than the occurrence of related forms in eastern Victoria and southeastern New South Wales.

In eastern Victoria, Long (1983b: fig. 3) used the appearance of Bothriolepis and phyllolepids to define the base of the Upper Devonian, with Groenlandaspis occurring in the latter half of the Frasnian. The fish fauna in the Boyd Volcanic Complex (Fergusson et al., 1979; Young, 1982, 1983), which as well as Culmacanthus includes at least four taxa (Bothriolepis, Pambulaspis, Antarctilamna, phyllolepids) in common with the Aztec fauna, apparently lacks Groenlandaspis. The fact that both Bothriolepis and Groenlandaspis in the Aztec Siltstone occur in the lowest fossiliferous beds, and far below the phyllolepid zone, indicates again that these are earlier occurrences than the range of these forms in southeastern Australia. In western New South Wales and central Australia groenlandaspid arthrodires are associated with thelodont scales in the Wuttagoonaspis fauna (Ritchie, 1975; Turner et al., 1981) but the only antiarchs from this fauna are asterolepids (Young, 1984a), so this appears to be older than the Aztec fauna. An Early-Middle Devonian age has been assigned to the *Wuttagoonaspis* fauna, but the occurrence of the Antarctic shark Mcmurdodus (Turner and Young, 1987), otherwise only known from the Aztec Siltstone, may indicate less difference in age to the lower Aztec fauna than previously thought.

In southeastern New South Wales the Boyd Volcanic Complex provides evidence for a minimum age for the Aztec fauna, because the overlying Merrimbula Group contains a marine invertebrate fauna of probable late Frasnian age (e.g. Roberts et al., 1972). A single early Late Devonian marine transgression in southeastern Australia may be assumed, for which the oldest reliable age is late Frasnian based on upper gigas Zone conodonts (Pickett, 1972). This implies a late Givetian – early Frasnian age for the underlying fishes and equivalent faunas in eastern Victoria, and an approximate younger limit to the age of the Aztec Siltstone based on the phyllolepid placoderms in its upper horizons. However, although the Victorian and southern New South Wales fish successions are broadly equivalent in age, detailed taxonomic work on placoderms common to the two areas (e.g. bothriolepids, phyllolepids) has not yet been done. The results of the present study show specific differences between the Culmacanthus remains from the two sequences, which may provisionally be regarded as indicating difference in age, but there is as yet no reliable evidence on which occurrence is the older. It should also be noted that according to Long (1983a) the culmacanthid from Freestone Creek is not conspecific with C. stewarti, although other species (e.g. Bothriolepis cullodenensis Long,

1983b) are shared between the two assemblages. Further detailed taxonomic work on the placoderms in the various faunas from southeastern New South Wales and Victoria should clarify the precise correlation between the two sequences.

## Biogeography

The biogeography of the Aztec fish fauna has been discussed previously by Young (1981, 1982, 1984b, 1988) and Grande and Eastman (1986), whilst Long (1986a) has recently commented on acanthodian biogeography in the Devonian. The presence of species of Culmacanthus in southeastern Australia and southern Victoria Land, Antarctica, but nowhere else, corresponds with the pattern indicated previously by the elasmobranch Antarctilamna (Young, 1982), the antiarch Pambulaspis (Young, 1988), and possibly the placoderm Antarctaspis (if a relationship to phyllolepids is confirmed; see Young, 1987: fig. 5). These distributions are all consistent with grouping the two regions together in an 'East Gondwana Province' as proposed by Young (1981). It should also be noted that the only two fish assemblages recorded from any continent in which bothriolepid antiarchs and turiniid thelodonts are associated are in southeastern Australia and southern Victoria Land, and species group interrelationships for the cosmopolitan antiarch Bothriolepis again indicate an Antarctica-Australia connection (Young, 1988). All these fishes inhabited freshwater environments, but this does not mean that they were unable to cross marine barriers, and in this respect no specific data are provided on the Devonian palaeogeography of the Antarctic-Australian region. It is relevant to note however that the distinctive dermal cheek plates of Culmacanthus have not been found in the well-studied fish faunas from the classic Old Red Sandstone localities of the Northern Hemisphere, but that they do occur in the Southern Hemisphere in two areas separated today by the vast expanse of the Southern Ocean, and a distance in excess of 4500km, which exceeds by a considerable margin the 3000km-wide ocean postulated by some authors to have separated Gondwana from Euramerica during the Late Devonian. Thus the evidence of culmacanthid distribution is entirely consistent with reconstructions of a Palaeozoic Gondwana which minimize or remove oceanic barriers by juxtaposing southeastern Australia and Victoria Land (Fig. 1).

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PROC. LINN. SOC. N.S.W., 111 (1), 1989

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